



## Recovery of arbuscular mycorrhizal fungi root colonization after severe anthropogenic disturbance: four species assessed in old-growth Mediterranean grassland

R. Jaunatre, N. Fonvieille, T. Spiegelberger, Elise Buisson, Thierry Dutoit

### ► To cite this version:

R. Jaunatre, N. Fonvieille, T. Spiegelberger, Elise Buisson, Thierry Dutoit. Recovery of arbuscular mycorrhizal fungi root colonization after severe anthropogenic disturbance: four species assessed in old-growth Mediterranean grassland. *Folia Geobotanica*, 2016, 51 (4), pp.319 - 332. 10.1007/s12224-016-9254-z . hal-01473741

**HAL Id: hal-01473741**

**<https://hal.science/hal-01473741>**

Submitted on 4 May 2018

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title Page

**Title: Recovery of arbuscular mycorrhizal fungi root colonization after severe anthropogenic disturbance: four species assessed in old-growth Mediterranean grassland.**

Short title: Arbuscular mycorrhizal root colonization recovery after disturbance

Authors:

Renaud Jaunatre (corresponding author)

Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE), Université d'Avignon et des Pays de Vaucluse, UMR CNRS IRD Aix Marseille Université, IUT, Agroparc, BP 61207, F-84000 Avignon Cedex 9, France

Irstea, UR EMGR Mountain Ecosystems, 2 rue de la papeterie, F-38400 Saint Martin d'Hères, France

University Grenoble Alpes, F-38402 Grenoble, France

[renaud.jaunatre@irstea.fr](mailto:renaud.jaunatre@irstea.fr)

Telephone number: +33 4 76 76 28 11

Fax number: +33 4 76 51 38 03

Noellie Fonvieille

Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE), Université d'Avignon et des Pays de Vaucluse, UMR CNRS IRD Aix Marseille Université, IUT, Agroparc, BP 61207, F-84000 Avignon Cedex 9, France

Thomas Spiegelberger

Irstea, UR EMGR Mountain Ecosystems, 2 rue de la papeterie, F-38400 Saint Martin d'Hères, France

University Grenoble Alpes, F-38402 Grenoble, France

Ecole Polytechnique Fédérale de Lausanne (EPFL), Laboratory of Ecological Systems (ECOS), Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Research Group Restoration Ecology, Site Lausanne, Station 2, 1015 Lausanne, Switzerland

Elise Buisson

Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE), Université d'Avignon et des Pays de Vaucluse, UMR CNRS IRD Aix Marseille Université, IUT, Agroparc, BP 61207, F-84000 Avignon Cedex 9, France

Thierry Dutoit

Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE), Université d'Avignon et des Pays de Vaucluse, UMR CNRS IRD Aix Marseille Université, IUT, Agroparc, BP 61207, F-84000 Avignon Cedex 9, France

Title: Recovery of arbuscular mycorrhizal fungi root colonization after severe anthropogenic disturbance: four species assessed in old-growth Mediterranean grassland.

Renaud Jaunatre<sup>a,b</sup> (corresponding author), Noellie Fonvieille<sup>a</sup>, Thomas Spiegelberger<sup>b,c</sup>, Elise Buisson<sup>a</sup> & Thierry Dutoit<sup>a</sup>

<sup>a</sup>Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE),

Université d'Avignon et des Pays de Vaucluse,

UMR CNRS IRD Aix Marseille Université

<sup>b</sup>Université Grenoble Alpes, Irstea, UR EMGR

<sup>c</sup>Ecole Polytechnique Fédérale de Lausanne (EPFL), Laboratory of Ecological Systems (ECOS) - Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Research Group Restoration Ecology

Current corresponding address

Irstea, 2 rue de la papeterie, 38 400 Saint Martin d'Hères, France

Fax number: +33 4 7651 38 03

Email: [renaud.jaunatre@irstea.fr](mailto:renaud.jaunatre@irstea.fr)

### Abstract

Arbuscular mycorrhizal fungi (AMF) interact continuously with vegetation and soil and thus shape the dynamics of plant communities. Yet the recovery of AMF after severe anthropogenic disturbance such as cultivation has rarely been assessed. Here, to determine whether AMF root colonization recovers after such disturbance, we compared AMF root colonization in abandoned fields last cultivated 2, 35, and 150 years ago in the La Crau area (south-eastern France) with that of a grassland several thousands of years old (considered as the reference ecosystem). We measured AMF root colonization of four species (*Carthamus lanatus* L., *Carduus pycnocephalus* L., *Brachypodium distachyon* (L.) P. Beauv., and *Bromus madritensis*), and performed surveys of plant communities and soil chemical properties. AMF root colonization was still significantly lower 35 years after disturbance for one species (*B. distachyon*) and 2 years after disturbance for two species (*B. distachyon* and *B. madritensis*). The main soil chemical properties (soil pH, phosphorus and potassium content) were similar to the reference ecosystem 35 years after disturbance. Average vegetation height and cover recovered after 35 years, whereas species richness recovered only on the field abandoned for 150 years. Vegetation composition and structure did not recover in any of the abandoned fields. Our results suggest that recovery of AMF root colonization is very low after a severe anthropogenic disturbance, despite the recovery of soil chemical properties.

Key Words: Cultivation; Diversity; Plant Community; Steppe; Arbuscular Mycorrhizal Fungi

## Introduction

The importance of taking into account arbuscular mycorrhizal fungus (AMF) interactions when exploring plant community dynamics is increasingly acknowledged (Grime et al. 1987; O'Connor et al. 2002; van der Heijden and Horton 2009; Bever et al. 2010; Koziol and Bever 2015). However, there are far fewer studies of AMF than of plants because access to AMF data is more difficult (Bever et al. 2001). Mycorrhizas can be found in most plant communities (van der Heijden and Sanders 2002), principally arbuscular mycorrhizal fungi (AMF), and interact with 80% of plant species (Wang and Qiu 2006). AMF increase plant water and phosphorus uptake mainly through the increased soil volume available for foraging (Allen 1982; Bolan 1991; Koide 1991; Augé 2001) and may thus impact growth of plant individuals and of their descendants (Koide and Lu 1992; Heppell et al. 2002). Consequently, AMF modify competition between plants, thereby affecting their coexistence (Grime et al. 1987; Smith et al. 1999; Mariotte et al. 2012) as well as the structure (Wilson and Hartnett 1997; O'Connor et al. 2002), species richness and composition of plant communities (Gange et al. 1993; Francis and Read 1994; Zobel and Moora 1995). This makes AMF dynamics a key to improving our comprehension of ecosystem functioning, and a topic that clearly warrants further investigation. Ecosystems in stressful environments are known to favor biotic interactions such as facilitation within plant species (Callaway et al. 2002; He et al. 2013) or with AMF (van der Heijden et al. 2003), especially old-growth grasslands. These ancient grassland ecosystems characterized by high species richness, high endemism, and unique species composition (Veldman et al. 2015) have had time to develop species-specific relationships with soil organisms (Tscherko et al. 2005; Bauer et al. 2015).

Such old-growth grasslands (e.g. dehesa in Spain or continental steppes in Siberia) are particularly threatened. Technical progress in agronomy in the last century allowed agricultural intensification in low-productivity ecosystems (Huston 2005). Understanding how such changes in land-use can alter these ecosystems is important, especially when environmental authorities aim to stop biodiversity loss and target 15% ecosystem restoration (Millennium Ecosystem Assessment 2005; Convention on Biological Diversity 2011). In this context, abandonment of intensive land-use can be viewed as an opportunity both to restore former ecosystems and to study ecosystem natural recovery (Prach and Walker 2011). While old-growth grasslands usually show poor recovery after severe anthropogenic disturbance (Forey and Dutoit 2012; Veldman et al., 2015), little seems to be known about the recovery of other ecosystem components, such as soil or AMF.

Cultivation can be seen as a severe anthropogenic disturbance for natural or semi-natural plant communities: during cultivation, disturbance occurs over a large scale exceeding plant community processes (Peterson et al. 1998; Huston 1999) and its strength (i.e. the force of the disturbance; Sousa 1984) is high. The severity of disturbance (i.e. the damage caused by the disturbance; Sousa 1984) is also high, as the majority of mature plants initially present are killed prior to and during a cultivation event. As a consequence, anthropogenic disturbance such as cultivation is followed by low recovery in many ecosystems, such as grasslands, heathlands or forests (Bellemare et al. 2002; Dupouey et al. 2002; Römermann et al. 2005; Elmore et al. 2007; Gustavsson et al. 2007). In the medium term (i.e. decades), vegetation recovery has been proven to be very poor (Römermann et al. 2005; Buisson et al. 2006). Cultivation disturbance generally leads to leaching of amended nutrients and therefore a progressive recovery of soil chemical properties, except for phosphorus, which is known to remain in soil (Smits et al. 2008; Henkin et al. 2010). Due to their low dispersal and competitive abilities, most steppe plant species can recolonize only a few meters from remnant steppe patches (Buisson et al. 2006). This means recovery of vegetation composition is usually poor even when abandoned fields are surrounded by remnant steppe patches.

To address AMF recovery dynamics, we chose the La Crau area of south-eastern France, an old-growth Mediterranean dry grassland or steppe plant community impacted by thousands of years of interaction between (1) Mediterranean climate, (2) a particularly well-draining soil and (3) extensive sheep grazing (Devaux et al. 1983; Buisson and Dutoit, 2006). Almost 20% of this species-rich plant community was once cultivated and then abandoned. As AMF root colonization depends not only on AMF dispersal abilities but also on host abundance and soil conditions, our hypothesis was that the more recent and intense the disturbance is, the less AMF root colonization recovers.

We assessed AMF root colonization on four plant species from this Mediterranean steppe after three disturbance events (a vineyard abandoned for 150 years, a melon field abandoned for 35 years and an intensive orchard abandoned for 2 years), compared to an undisturbed ecosystem, to determine whether AMF root colonization recovers after cultivation disturbance.

## Materials and methods

### Study area

The La Crau area is the last xeric steppe of south-eastern France (ca. 10,000ha). It is shaped by i) a dry Mediterranean climate, ii) a 40cm-deep soil with about 50% of siliceous stones overlying an almost impermeable conglomerate layer, making the alluvial water table unavailable to plant roots and iii) itinerant sheep grazing over a period of several thousand years (Devaux et al. 1983; Buisson and Dutoit 2006). This has led to a unique and species-rich vegetation association composed mainly of annuals and dominated by *Brachypodium retusum* Pers.

and *Thymus vulgaris* L.. The steppe, which experienced recurring anthropogenic disturbance until 400 BP from sheep grazing and pastoral fires, has lost more than 80% of its original 45,000 ha area due to other anthropogenic disturbances such as intensive cultivation (Buisson and Dutoit 2006). Our study focuses on three types of cultivation, all initiated on the original steppe, applied for several years and today abandoned: (1) a vineyard abandoned approximately 150 years ago (AF-150) as revealed from consultation of old cadastral maps and land registers (Dutoit et al. 2005), (2) two melon fields, cultivated for one year only before being abandoned 35 years ago (AF-35) (Römermann et al. 2005) and an orchard cultivated for 17 years, abandoned in 2006 and which underwent its last disturbance comparable to ploughing in 2009, two years before sampling (Jaunatre et al. 2014) (AF-2) (Fig. 1). The control was the surrounding steppe, whose available history (Cassini et al. 1778) showed no severe anthropogenic disturbance. The three types of cultivation represent a gradient both of time since abandonment and of disturbance intensity: the vineyard probably underwent only one ploughing and no herbicide applications (Dutoit et al. 2005), the melon field underwent one ploughing and one fertilizer and herbicide application (Römermann et al. 2005), while the orchard underwent repeated ploughing, fertilizer and herbicide applications (Jaunatre et al. 2014).

## 2.2. Sampling

We concentrated our sampling areas around the former vineyard (AF-150, n=3) and the former orchard (AF-2, n=3) as they are unique in the La Crau area (Fig. 1). Two steppe sites (ST-6000, n=6) and two sites in fields abandoned for 35 years (AF-35, n=6) were selected, one of each in proximity to either AF-150 or AF-2. The imbalance in design is due to the fact that there was only one site abandoned for 150 years before sampling and only one site abandoned for 2 years before sampling in the entire La Crau area (10 000 ha). We considered the distance between sampling areas (>70m; Fig 1c) sufficient because of the very weak dispersal ability of La Crau plant species (i.e. after 19 years of abandonment, half the species had colonized less than a few meters, Buisson and Dutoit 2004; Buisson et al., 2006). In each of the six sites selected, three sampling areas were set up to sample AMF root colonization, vegetation and soil (Fig. 1d).

### AMF root colonization

Colonization by AMF was assessed from roots of four species occurring over almost the entire gradient described above: i) *Carthamus lanatus* L, an Asteraceae more abundant in the steppe, ii) *Carduus pycnocephalus* L, an Asteraceae more abundant in the abandoned fields, iii) *Brachypodium distachyon* (L.) P. Beauv, a Poaceae more abundant in the steppe and iv) *Bromus madritensis* L, a Poaceae more abundant in the abandoned fields. When possible, in each sampling area three individuals of each species were collected; however, some species were not present in some sampling areas. Air-dried roots were colored with black Schaeffer ink using the vinegar coloration method (Vierheilig et al. 1998). For total percentage AMF root colonization, internal hyphae, vesicles or arbuscules were counted with the magnified intersections method using 100 intersections (McGonigle et al. 1990).

### Soil analyses

In each sampling area, three 70g sub-samples of soil were taken from depths of 1-10cm (Fig. 1d) and pooled to constitute one soil sample. Soil was sieved (2mm mesh) for analyses carried out by INRA (*Institut National de la Recherche Agronomique*, Arras, France). Granulometry without decarbonation (percentage content of clay (<0.002 mm), fine silt (0.002-0.02 mm), coarse silt (0.02-0.05 mm), fine sand (0.05-0.2 mm) and coarse sand (0.2-2 mm)), nutrients (organic C, total N, P<sub>2</sub>O<sub>5</sub> (Olsen et al. 1954), CaO, and K<sub>2</sub>O) and pH were measured according to the methods described in Baize (2000).

### Vegetation survey

Vegetation relevés were performed on three 2x2m quadrats for each sampling area using Braun-Blanquet coefficients (Braun-Blanquet et al. 1952). In addition, average vegetation height (i.e. height of the dominant stratum) and cover (in percentage) were estimated in each quadrat.

### Data analysis

Generalized Linear Mixed Models (GLMM) were used to determine whether the cultivation disturbance continued to affect AMF root colonization, soil chemical variables and plant community characteristics. We compared two models: in the first, age was implemented as a categorical fixed factor and blocks (i.e. around the AF-2 or around AF-150; Fig. 1) as a categorical random factor; the second contained neither a fixed factor nor blocks as a categorical random factor. If the first model containing age had a lower Aikake Information Criterion (AIC) with a difference greater than 2, age effect was declared significant (Burnham and Anderson 2004) and difference between ages was assessed by a multiple comparison test using Tukey's method. To obtain a global overview of soil parameters and of plant communities, we ran a Principal Component Analysis (PCA) for soil parameters and a Correspondence Analysis (CA) for plant community (Borcard et al. 2011). To measure similarity of plant communities to those of the undisturbed control, we used the normalized Community Structure Integrity Index (CSII<sub>norm</sub>) and the Higher Abundance Index (HAI) to distinguish the percentage of recovery of reference species abundances (CSII<sub>norm</sub>) from new abundances not occurring in this reference (HAI) (Jaunatre et al., 2013).

All analyses were performed with R 2.13.0 (R Development Core Team 2011), univariate analyses with its package "lme4" and "multcomp" (Hothorn et al. 2008; Bates et al. 2012) and multivariate analyses with its packages "ade4" (Chessel et al. 2004; Dray and Dufour, 2007; Dray et al. 2007) and "vegan" (Oksanen et al. 2008).

## Results

### AMF root colonization

AMF root colonization recovered to ST-6000 values (approximately 90%) in all three abandoned fields for forbs (*Carthamus lanatus* and *C. pycnocephalus*; Fig. 2, Table 1). However, both grasses did not recover in all the locations: *Bromus madritensis* shows lower AMF root colonization in AF-2 ( $40.7 \pm 3.8$ ) than in ST-6000 ( $63.9 \pm 4.2$ ) (Fig. 6, Table 1) and *B. distachyon* shows a significant difference in AMF root colonization between AF-35 ( $51.4 \pm 5.9$ ) and ST-6000 ( $64.2 \pm 2.1$ ) (no *B. distachyon* was found in AF-2).

### Soil analyses

The PCA of soil properties (Fig. 3) clearly discriminates among the four locations. The first axis (35.2%) shows a clear distinction in age between the field abandoned 2 years previously (AF-2) and the three other locations, with higher concentrations of  $P_2O_5$ , pH and  $K_2O$  (Fig. 4), although only pH is significantly higher (Table 1). The second axis (24.5%) discriminates the steppe (ST-6000) from the longest-abandoned field (AF-150), with higher carbon and nitrogen content (Fig. 4), although only carbon differences are significant (Table 1).

### Vegetation survey

Compared to the reference, all three abandoned fields have significantly different values for composition and structure (Table 1, Fig. 5). Their CSII<sub>norm</sub> is lower: AF-150 and AF-35 have recovered less than 60% of the vegetation structure, while AF-2 has recovered less than 20%. Their HAI is higher: in AF-150 and AF-35, 50% of the structure is composed of species whose abundances are higher than in ST-6000 (both new species and the same species); while in AF-2, more than 70% of species have abundances higher than in ST-6000. These differences in plant community variables are also discernible on the correspondence analysis (Fig. 6): AF-2 is dominated by *Bromus madritensis* L., *Bromus lanceolatus* Roth and *Carduus pycnocephalus* L.. AF-35 is also characterized by Poaceae and Asteraceae (*Bromus hordeaceus* L., *Bromus rubens* L., *Carthamus lanatus* L. etc.). AF-150 and ST-6000 share many species (e.g. *Aegilops ovata* L., *Brachypodium distachyon* (L.) P. Beauv., *Carlina corymbosa* L., *Erodium cicutarium* (L.) L'Hérit. or *Plantago bellardii* All.), although i) some dominant ST-6000 species are absent from AF-150 (e.g. *Brachypodium retusum* (Pers.) P. Beauv.) and ii) some AF-150 species are absent from ST-6000 (e.g. *Bothriochloa ischaemum* (L.) Keng, *Crucianella angustifolia* L.). The species richness of AF-150 is not significantly different from that of ST-6000; however, it is significantly lower for AF-35 and AF-2. All the abandoned field locations except AF-2 have recovered ST-6000 average height and vegetation cover, while AF-2 shows significantly higher values (Table 1, Fig. 5).

## Discussion

It takes a very long time to recover ecosystem characteristics. This has been proved for many different old-growth grassland types, such as Midwest prairie, Scandinavian semi-natural grasslands, Mediterranean steppe or limestone grassland (Tomanek et al. 1955; Bonet et Pausas 2004; Öster et al. 2009; Forey and Dutoit 2012), and our study confirms it. Most of these low-resilient ecosystems have similar characteristics: harsh environmental conditions, which are attenuated by the disturbance event (i.e. nutrient or water availability is increased). In such a context, some plant species adapted to higher nutrient content can colonize and generate relatively stable mutualistic associations with soil organisms, such as AMF or microbial communities, thus slowing down the potential recovery of the original state (Spiegelberger et al. 2006; Wardle et al. 2014). Our study shows that it is not only vegetation and soil components that are durably affected by a severe anthropogenic disturbance such as cultivation: there is an impact on AMF root colonization too. The results also confirm our hypothesis that the more recent and intense the disturbance is, the less AMF root colonization recovers. Our findings are in line with those from studies on different components under harsh environmental conditions, which reacted in a similar way (Hejcman et al. 2007; Spiegelberger et al. 2010, 2006). However, new evidence is provided here on ecosystem recovery via the recovery of AMF root colonization, rarely studied in parallel with soil and plant communities.

### AMF root colonization

AMF root colonization can decrease due to any soil disturbance (Jasper et al. 1989). Agricultural practices in particular are known to impact AMF communities, modifying their abundance, their diversity and their composition (Douds et al. 1995; Jansa et al. 2003), and their reproduction dynamics (Oehl et al. 2009). Areas cultivated with more fertilizer show less AMF root colonization (Douds et al. 1995; Mäder et al. 2000). In our study, the AMF root colonization rate increases with time since cultivation abandonment for two plant species out of four. It has previously been shown that AMF root colonization can recover with time (Eriksson 2001; Gibson-Roy et al. 2014) but that this depends on plant community composition (Fitzsimons et al. 2008). This is supported by our results: AMF root colonization recovered and was no longer significantly different from the steppe after 35 years, except for *B. distachyon*, and the field abandoned for 35 years showed over 50% recovery of plant community structure (Figure 5). It should be noted that the major finding here is the difference between AMF root colonization in abandoned fields and in the reference. The similar values found here for AMF root colonization may in fact mask an absence of recovery of certain AMF species, since it is likely that different AMF species are involved. This hypothesis is supported by the fact that AMF community composition can be altered by a change in plant community composition (Klamer and Hedlund, 2004), and such a change occurred in our abandoned fields. We did not find any difference in root colonization recovery between species more abundant in the steppe (C.

*lanatus* and *B. distachyon*) and species more abundant in the abandoned fields (*C. pycnocephalus* and *B. madritensis*). We found, however, that grasses (*B. distachyon* and *B. madritensis*) have higher average mycorrhizal root colonization and higher recovery of mycorrhizal root colonization than forbs (*C. lanatus* and *C. pycnocephalus*), which confirms that plant functional type is the most important driver of plant response to mycorrhizal fungi (Hoeksema et al. 2010).

#### Soil parameters

The different abandoned fields are found to have contrasting soil properties. The former vineyard, which is the longest abandoned field, has the lowest pH and potassium and phosphorus content. However, the difference in fertilization practices can also introduce biases; fertilizer use was more sparing and more organic-based 150 years ago than 3 years ago (Dutoit et al. 2005). Annual, and therefore cumulative, fertilizer quantities are difficult to estimate. Despite these potential biases, our results are consistent with findings from other studies: as in Wong et al. (2010), potassium and phosphorus content tend to decrease with time since last cultivation, and as in studies on Mediterranean or calcareous grasslands (Smits et al. 2008; Henkin et al. 2010), high soil phosphorus content is maintained even 35 years after cessation of fertilization. Soil properties are known to be very important in determining plant community diversity, structure and composition. For instance, Kulmatiski et al. 2006 showed how soil legacies impact invasive plant species distributions and Janssens et al. (1998) suggested that 5 mg of phosphorus per 100 g of dry soil is a threshold value limiting establishment of species-rich plant communities. Despite the fact that in our abandoned fields current soil phosphorus content remains close to (AF-2) or below this level (AF-35 and AF-150), it is possible that a previous higher phosphorus content had a long-term effect which can still be observed, even after the recovery of lower values (Semelová et al. 2008).

#### Plant communities

As with soil, the longer the time since abandonment, the more plant community characteristics in abandoned fields differ from the reference. More recently abandoned fields have lower species richness or CSII, while they have higher HAI, average vegetation height and cover. Moreover, vegetation composition, which is mainly dominated by grasses such as *Bromus* spp. in the most recently abandoned fields, gains in species richness and in the number of forbs with time since abandonment. Similar slow recolonization was observed in other ecosystems after severe disturbances (Tomanek et al. 1955; Coffin et al. 1996; Meiners et al. 2002; Bonet and Pausas 2004). However after 150 years, while the vegetation composition of the abandoned field is close to that of the steppe it is still slightly different, notably due to the absence of *B. retusum*, the dominant steppe species. Interestingly, the species with the lowest AMF root colonization recovery rate (*B. distachyon*) is phylogenetically closest to *B. retusum* (The Angiosperm Phylogeny Group 2009). *B. retusum* is not present in any part of this long-abandoned field, although it is the dominant steppe species and occurs at the abandoned field boundaries, and despite the fact that all measured environmental characteristics are not significantly different. Low seed production and fertility, and hence poor dispersal abilities, have already been hypothesized (Buisson et al. 2006; Coiffait-Gombault et al. 2012). The slow recovery of AMF root colonization rates in a phylogenetically close species would suggest that *B. retusum* not only has low seed production (Caturla et al. 2000) but also suffers from a lack of AMF interaction. This interaction would likely enhance its growth by higher phosphorus uptake (López-Sánchez et al. 1992), enabling it to establish in abandoned fields.

#### Ecosystem recovery

Our results on vegetation are consistent with previous studies, where: vegetation was still affected 70 years after a fertilization event, even though the soil almost recovered its properties (Spiegelberger et al. 2006); only half the species were able to colonize abandoned fields 50 years later (Öster et al. 2009); or differences in plant communities were still significant more than 2000 years after a cultivation event in a forest community (Dupouey et al. 2002). The filter model is often used to describe vegetation dynamics (Keddy 1992; Lortie et al. 2004): i) plant species have to be able to disperse, which depends on species dispersal abilities and proximity of source site (Gibson and Brown 1991; Pärtel and Zobel 1999; Lindborg and Eriksson 2004; Herault and Thoen 2009); ii) plant species have to be able to withstand environmental constraints, which depends both on historical environmental conditions and on disturbance legacies (Foster et al. 2003) and iii) the first two filters will be modified by biotic interactions and will depend on the presence of facilitators or competitors in the community (Bruno et al. 2003). This model explains the low resilience of plants after cultivation in the La Crau area: species have low dispersal abilities and no permanent seed bank (Graham and Hutchings 1988; Römermann et al. 2005), soil nutrient content is still different in recently abandoned fields, and finally, some species are better competitors under higher nutrient conditions (Baeten et al. 2009; Öster et al. 2009), especially if they arrived first due to chance or better dispersal abilities (Fukami et al. 2005).

It should be feasible to apply a similar model to AMF, to explain their recovery after a severe anthropogenic disturbance, as suggested by Lekberg et al. (2007). If AMF have been eliminated during the cultivation event (Douds et al. 1995; Jansa et al. 2003), they have to disperse through the disturbed area. Wind seems to be a poor long-distance disperser (Egan et al., 2014), but faunal agents may also provide some local-scale dispersal (Warner et al. 1987; Allen 1989; Harinikumar and Bagyaraj 1994). Hyphae not killed by cultivation can also be a rich source of AMF; however, they are highly affected by soil disturbance (Jasper et al. 1989; Brundrett and Abbott,

1994). AMF root colonization thus depends on environmental conditions: the more available nutrients are, the less roots are colonized by AMF (Koide, 1991). Our findings support this: AMF root colonization was higher in the abandoned fields with lower soil nutrient content. Finally, AMF root colonization depends on biotic interactions. In our study, the abandoned field with the highest vegetation average height and the highest vegetation cover (AF-2) was found to have the lowest mycorrhizal root colonization. These results are in accordance with the negative relationship between vegetation biomass and AMF biomass already found in abandoned fields (Hedlund et al., 2003). Despite the fact that mechanical soil disturbance plays a greater role than plant communities in shaping AMF communities (Schnoor et al. 2011), plant species richness has been shown to increase the diversity and fitness of AMF (Burrows and Pfleger, 2002). Moreover, the diversity of AMF infecting an individual plant depends on the diversity of the whole plant community (van de Voorde et al. 2010), and the composition of the plant community has a significant effect on the composition of the AMF community (Johnson, 1993; Eom et al. 2000; Hiiesalu et al., 2014).

Our study is a first step towards exploring the relationship between a proxy of AMF (AMF root colonization), soil conditions and plant communities. In accordance with our hypotheses, recovery of these three ecosystem components differs, increasing from vegetation (lowest recovery) to AMF root colonization (intermediate recovery), to soil conditions (highest recovery). All three components assessed are moving towards the undisturbed state, but full, unassisted recovery is highly unlikely within a human lifetime.

Feedbacks occurring between different ecosystem components, as in a panarchy model, need to be taken into account to understand the overall recovery process. One component starts to recover while being influenced by another component; based on these dynamics, the recovery of the first component is affected, and in turn the recovery of other components is further influenced (Allen et al. 2014). To our knowledge, although few studies have measured the recovery of different components of an ecosystem after disturbance, most of them found, like us, staggered responses for each component (García-Tejero et al. 2013; Wardle and Jonsson, 2013). Determining the limiting components able to affect, slow down or stop the recovery dynamics of the whole ecosystem would be of particular interest in a restoration context. AMF communities affect plant communities in complex ways: like plants, not all AMF species play the same role in ecosystems (Hart et al. 2003). The effects of AMF on plants are species-specific (Hoeksema et al. 2010; Endresz et al. 2013), but also depend on environmental conditions (Grime et al. 1987; Hartnett and Wilson, 1999; Kytöviita et al. 2003), and higher AMF root colonization is not always linked with better vegetation recovery (Richter et al. 2002). Further research is required to explore how different ecosystem components can affect overall ecosystem recovery, and how they could be used to facilitate or to accelerate this recovery in a restoration context (Allen, 1989; Herrera et al. 1993; Callaway et al. 2001; Kardol et al. 2009).



347 **Acknowledgement**

348 This study was supported by CDC Biodiversité, CEN PACA, the Réserve Naturelle des Coussouls de Crau, the  
349 Conseil Régional de Provence Alpes Côtes d’Azur and CNRS RTP Ingecotech funding. The author would like to  
350 thank Daniel Pavon (IMBE) for help with fieldwork and Marjorie Sweetko for English language editing.

## References

- Allen CR, Angeler DG, Garmestani AS, Gunderson LH, Holling CS (2014) Panarchy: Theory and Application. *Ecosystems* 17:578-589
- Allen EB (1989) The restoration of disturbed arid landscapes with special reference to mycorrhizal fungi. *J Arid Environ* 17:279-286
- Allen MF (1982) Influence of Vesicular-Arbuscular Mycorrhizae on Water Movement Through *Bouteloua gracilis* (HBK) Lag Ex Steud. *New Phytol* 91:191-196
- Augé RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11:3-42
- Baeten L, Jacquemyn H, Van Calster H, Van Beek E, Devlaeminck R, Verheyen K, Hermy M (2009) Low recruitment across life stages partly accounts for the slow colonization of forest herbs. *J Ecol* 97:109-117
- Baize D (2000) Guide des analyses en pédologie. INRA, Paris
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <http://CRAN.R-project.org/package=lme4>
- Bauer JT, Mack KML, Bever JD (2015) Plant-soil feedbacks as drivers of succession: evidence from remnant and restored tallgrass prairies. *Ecosphere*, 6:art158 <http://dx.doi.org/10.1890/ES14-00480.1>
- Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *J Biogeogr* 29:1401-1420
- Bever JD, Dickie IA, Facelli E, Facelli JM, Klironomos J, Moora M, Rillig MC, Stock WD, Tibbett M, Zobel M (2010) Rooting theories of plant community ecology in microbial interactions. *Trends Ecol Evol* 25:468-478
- Bever JD, Schultz PA, Pringle A, Morton JB (2001) Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. *BioScience* 51:923-932
- Bolan NS (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant Soil* 134:189-207
- Bonet A, Pausas J (2004) Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. *Plant Ecol* 174:257-270
- Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer, New York
- Braun-Blanquet J, Roussine N, Nègre R, Emberger L (1952) Les groupements végétaux de la France Méditerranéenne. CNRS, Paris
- Brundrett MC, Abbott LK (1994) Mycorrhizal fungus propagules in the jarrah forest. *New Phytol.* 127:539-546
- Bruno JF, Stachowicz JJ, Bertness MD (2003). Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119-125
- Buisson E, Dutoit T (2004) Colonisation by native species of abandoned farmland adjacent to remnant patch of Mediterranean steppe. *Plant Ecol* 174:371-384.
- Buisson E, Dutoit T (2006) Creation of the natural reserve of La Crau: Implications for the creation and management of protected areas. *J Environ Manage* 80:318-326
- Buisson E, Dutoit T, Torre F, Römermann C, Poschlod P (2006) The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes. *Agric Ecosyst Environ* 115:6-14
- Burnham KP, Anderson DR (2004) Multimodel inference Understanding AIC and BIC in Model Selection. *Sociol Methods Res* 33:261-304
- Burrows RL, Pfleger FL (2002) Arbuscular mycorrhizal fungi respond to increasing plant diversity. *Can J Bot* 80:120-130
- Callaway R, Newingham B, Zabinski CA, Mahall BE (2001) Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbours. *Ecol Lett* 4:429-433
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844-848
- Cassini JD, Cassini J, Cassini CF, Cassini D (1778) Carte de Cassini de la région d'Aix en Provence et Légende
- Caturla RN, Raventós J, Guàrdia R, Vallejo VR (2000) Early post-fire regeneration dynamics of *Brachypodium retum* Pers. (Beauv.) in old fields of the Valencia region (eastern Spain). *Acta Oecol* 21:1-12
- Chessel D, Dufour AB, Thioulouse J (2004) The ade4 package-I- One-table methods. *R News* 4:5-10
- Coffin DP, Lauenroth WK, Burke IC (1996) Recovery of Vegetation in a Semiarid Grassland 53 Years after Disturbance. *Ecol Appl* 6:538-555
- Coiffait-Gombault C, Buisson E, Dutoit T (2012) Are old Mediterranean grasslands resilient to human disturbances? *Acta Oecol.* 43:86-94
- Convention on Biological Diversity (2011) Ways and means to support ecosystem restoration
- Devaux JP, Archiloque A, Borel L, Bourrelly M, Louis-Palluel J (1983) Notice de la carte phyto-écologique de la Crau (Bouches du Rhône). *Biologie-Ecologie méditerranéenne* 10:5-54

410 Douds DD, Galvez L, Janke RR, Wagoner P (1995) Effect of tillage and farming system upon populations and  
411 distribution of vesicular-arbuscular mycorrhizal fungi. *Agric Ecosyst Environ* 52:111-118  
412 Dray S, Dufour AB (2007) The ade4 Package: Implementing the Duality Diagram for Ecologists. *J Stat Soft* 22:1-  
413 20  
414 Dray S, Dufour AB, Chessel D (2007) The ade4 package-II: Two-table and K-table methods. *R News* 7:47-52  
415 Dupouey JL, Dambrine E, Laffite JD, Moares C (2002) Irreversible Impact of past Land Use on Forest Soils and  
416 Biodiversity. *Ecology* 83:2978-2984  
417 Dutoit T, Forey E, Römermann C, Buisson E, Fadda S, Saatkamp A, Gaignard P, Trivelly E (2005) Rémanence  
418 des utilisations anciennes et gestion conservatoire des pelouses calcicoles de France. *Biotechnologie,*  
419 *Agronomie, Sociétés et Environnement* 9: 125-132.  
420 Egan C, Li D-W, Klironomos J (2014) Detection of arbuscular mycorrhizal fungal spores in the air across different  
421 biomes and ecoregions *Fung Ecol* 12:26-31  
422 Elmore AJ, Mustard JF, Hamburg SP, Manning SJ (2007) Agricultural Legacies in the Great Basin Alter  
423 Vegetation Cover, Composition, and Response to Precipitation. *Ecosystems* 9:1231-1241  
424 Endresz G, Somodi I, Kalapos T (2013) Arbuscular mycorrhizal colonisation of roots of grass species differing in  
425 invasiveness. *Community Ecol* 14:67-76  
426 Eom AH, Hartnett DC, Wilson GWT (2000) Host plant species effects on arbuscular mycorrhizal fungal  
427 communities in tallgrass prairie. *Oecologia* 122:435-444  
428 Eriksson Å (2001) Arbuscular mycorrhiza in relation to management history, soil nutrients and plant species  
429 diversity. *Plant Ecol* 155:129-137  
430 Fitzsimons MS, Miller RM, Jastrow JD (2008) Scale-dependent niche axes of arbuscular mycorrhizal fungi.  
431 *Oecologia* 158:117-127  
432 Forey E, Dutoit T (2012) Vegetation, soils and seed banks of limestone grasslands are still impacted by former  
433 cultivation one century after abandonment. *Community Ecol* 13:194-202  
434 Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The Importance of Land-Use  
435 Legacies to Ecology and Conservation. *BioScience* 53:77-88  
436 Francis R, Read DJ (1994) The contributions of mycorrhizal fungi to the determination of plant community  
437 structure. *Plant Soil* 159:11-25  
438 Fukami T, Martijn Bezemer T, Mortimer SR, Putten WH (2005) Species divergence and trait convergence in  
439 experimental plant community assembly. *Ecol Lett* 8:1283-1290  
440 Gange AC, Brown VK, Sinclair GS (1993) Vesicular-Arbuscular Mycorrhizal Fungi: A Determinant of Plant  
441 Community Structure in Early Succession. *Funct Ecol* 7:616-622  
442 García-Tejero S, Taboada Á, Tárrega R, Salgado JM, Marcos E (2013) Differential responses of ecosystem  
443 components to a low-intensity fire in a Mediterranean forest: a three-year case study. *Community Ecol*  
444 14:110-120  
445 Gibson CWD, Brown VK (1991) The nature and rate of development of calcareous grassland in Southern Britain.  
446 *Biol Conserv* 58:297-316  
447 Gibson-Roy P, McLean C, Delpratt JC, Moore G (2014) Do arbuscular mycorrhizal fungi recolonize revegetated  
448 grasslands? *Ecol Manage Rest* 15:87-91.  
449 Graham DJ, Hutchings MJ, (1988) A Field Investigation of Germination from the Seed Bank of a Chalk Grassland  
450 Ley on Former Arable Land. *J Appl Ecol* 25:253-263  
451 Grime JP, Mackey JML, Hillier SH, Read DJ (1987) Floristic diversity in a model system using experimental  
452 microcosms. *Nature* 328:420-422  
453 Gustavsson E, Lennartsson T, Emanuelsson M (2007) Land use more than 200 years ago explains current grassland  
454 plant diversity in a Swedish agricultural landscape. *Biol Conserv* 138:47-59  
455 Harinikumar KM, Bagyaraj DJ (1994) Potential of earthworms, ants, millipeds, and termites for dissemination of  
456 vesicular-arbuscular mycorrhizal fungi in soil. *Biol Fertil Soils* 18:115-118  
457 Hart MM, Reader RJ, Klironomos JN (2003) Plant coexistence mediated by arbuscular mycorrhizal fungi. *Trends*  
458 *Ecol Evol* 18:418-423  
459 Hartnett DC, Wilson GWT (1999) Mycorrhizae influence plant community structure and diversity in tallgrass  
460 prairie. *Ecology* 80:1187-1195  
461 He Q, Bertness MD, Altieri AH (2013) Global shifts towards positive species interactions with increasing  
462 environmental stress. *Ecol Lett* 16:695-706  
463 Hedlund K, Santa Regina I, Van der Putten WH, Lepš J, Díaz T, Korthals W, Lavorel S, Brown VK, Gormsen SR,  
464 Rodríguez Barrueco C, Roy J, Smilauer P, Smilauerová M, Van Dijk C (2003) Plant Species Diversity,  
465 Plant Biomass and Responses of the Soil Community on Abandoned Land across Europe: Idiosyncrasy or  
466 Above-Belowground Time Lags. *Oikos*, 103:45-58.  
467 Hejerman M, Klauisová M, Schellberg J, Honsován D (2007) The Rengen Grassland Experiment: Plant species  
468 composition after 64 years of fertilizer application. *Agric Ecosyst Environ* 122:259-266

- Henkin Z, Seligman NG, Noy-Meir I (2010) Long-term productivity of Mediterranean herbaceous vegetation after a single phosphorus application. *J Veg Sci* 21:979-991
- Heppell KB, Shumway DL, Koide RT (2002) The effect of mycorrhizal infection of *Abutilon theophrasti* on competitiveness of offspring. *Funct Ecol* 12:171-175
- Herault B, Thoen D (2009) How habitat area, local and regional factors shape plant assemblages in isolated closed depressions. *Acta Oecol* 35:385-392
- Herrera MA, Salamanca CP, Barea JM (1993) Inoculation of woody legumes with selected arbuscular mycorrhizal fungi and rhizobia to recover desertified Mediterranean ecosystems. *Appl Environ Microbiol* 59:129-133
- Hiiesalu I, Pärtel M, Davison J, Gerhold P, Metsis M, Moora M, Öpik M, Vasar M, Zobel M, Wilson SD (2014) Species richness of arbuscular mycorrhizal fungi: associations with grassland plant richness and biomass. *New Phytol* 203:233-244
- Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol Lett* 13:394-407
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. *Biometrical J* 50:346-363
- Huston MA (1999) Local Processes and Regional Patterns: Appropriate Scales for Understanding Variation in the Diversity of Plants and Animals. *Oikos* 86:393-401
- Huston MA (2005) The three phases of land-use change: implications for biodiversity. *Ecol. Appl.* 15:1864-1878
- Jansa, J, Mozafar A, Kuhn G, Anken T, Ruh R, Sanders IR, Frossard E (2003) Soil tillage affects the community structure of mycorrhizal fungi in maize roots. *Ecol Appl* 13:1164-1176
- Janssens F, Peeters A, Tallwin JRB, Bakker JP, Bekker RM, Fillat F, Oomes MJM (1998) Relationship between soil chemical factors and grassland diversity. *Plant Soil* 202:69-78
- Jasper DA, Abbott LK, Robson AD (1989) Soil disturbance reduces the infectivity of external hyphae of vesicular-arbuscular mycorrhizal fungi. *New Phytol* 112:93-99
- Jaunatre R, Buisson E, Muller I, Morlon H, Mesléard F, Dutoit T (2013) New synthetic indicators to assess community resilience and restoration success. *Ecol Indicators* 29:468-477.
- Jaunatre R, Buisson E, Dutoit T (2014) Can ecological engineering restore Mediterranean rangeland after intensive cultivation? A large-scale experiment in southern France. *Ecol Eng* 64:202-212
- Johnson NC (1993) Can Fertilization of Soil Select Less Mutualistic Mycorrhizae? *Ecol Appl* 3:749
- Kardol P, Bezemer TM, Putten WHVD (2009) Soil Organism and Plant Introductions in Restoration of Species-Rich Grassland Communities. *Restor Ecol* 17:258-269
- Keddy PA (1992) Assembly and Response Rules: Two Goals for Predictive Community Ecology. *J Veg Sci* 3:157-164
- Klamer M, Hedlund K (2004) Fungal diversity in set-aside agricultural soil investigated using terminal-restriction fragment length polymorphism. *Soil Biol. and Biochem.* 36:983-988.
- Koide RT (1991) Nutrient supply, nutrient demand and plant response to mycorrhizal infection. *New Phytol* 117:365-386
- Koide RT, Lu X (1992) Mycorrhizal infection of wild oats: maternal effects on offspring growth and reproduction. *Oecologia* 90:218-226
- Koziol L, Bever JD (2015) Mycorrhizal Response Trades off with Plant Growth Rate and Increases with Plant Successional Status. *Ecology* 96:1768-1774
- Kulmatiski A, Beard KH, Stark JM (2006) Soil history as a primary control on plant invasion in abandoned agricultural fields. *J Appl Ecol* 43:868-876
- Kytöviita MM, Vestberg M, Tuomi J (2003) A test of mutual aid in common mycorrhizal networks: established vegetation negates benefit in seedlings. *Ecology* 84:898-906
- Lekberg Y, Koide RT, Rohr JR, Aldrich-Wolfe L, Morton JB (2007) Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. *J Ecol* 95:95-105
- Lindborg R, Eriksson O (2004) Historical Landscape Connectivity Affects Present Plant Species Diversity. *Ecology* 85:1840-1845
- López-Sánchez ME, Díaz G, Honrubia M (1992) Influence of vesicular-arbuscular mycorrhizal infection and P addition on growth and P nutrition of *Anthyllis cytisoides* L. and *Brachypodium retusum* (Pers.) Beauv. *Mycorrhiza* 2:41-45
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI, Callaway RM (2004) Rethinking plant community theory. *Oikos* 107:433-438
- Mäder P, Edenhofer S, Boller T, Wiemken A, Niggli U (2000) Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic, biological) and high-input (conventional) farming systems in a crop rotation. *Biol Fertil Soils* 31:150-156

527 Mariotte P, Meunier C, Johnson D, Thébault A, Spiegelberger T, Buttler A (2012) Arbuscular mycorrhizal fungi  
528 reduce the differences in competitiveness between dominant and subordinate plant species. *Mycorrhiza*  
529 23:267-277

530 McGonigle TP, Miller MH, Evans DG, Fairchild GL, Swan JA (1990) A New Method which Gives an Objective  
531 Measure of Colonization of Roots by Vesicular-Arbuscular Mycorrhizal Fungi. *New Phytol* 115:495-501

532 Meiners SJ, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field successions:  
533 community patterns and associations. *Ecography* 25:215-223

534 Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: Biodiversity Synthesis, World  
535 Resources Institute, Washington DC

536 O'Connor PJ, Smith SE, Smith FA (2002) Arbuscular mycorrhizas influence plant diversity and community  
537 structure in a semiarid herbland. *New Phytol* 154:209-218

538 Oehl F, Sieverding E, Ineichen K, Mäder P, Wiemken A, Boller T (2009) Distinct sporulation dynamics of  
539 arbuscular mycorrhizal fungal communities from different agroecosystems in long-term microcosms. *Agric*  
540 *Ecosyst Environ* 134:257-268

541 Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Henry M, Stevens H, Wagner H (2008) vegan:  
542 Community Ecology Package. R package version 1.13-1

543 Olsen SR, Cole CV, Watanabe FS, Dean LA (1954) Estimation of available phosphorus in soils by extraction with  
544 sodium bicarbonate. U.S. Dep. Agric. Circ. 939

545 Öster M, Ask K, Römermann C, Tackenberg O, Eriksson O (2009) Plant colonization of ex-arable fields from  
546 adjacent species-rich grasslands: The importance of dispersal vs. recruitment ability. *Agric Ecosyst Environ*  
547 130:93-99

548 Pärtel M, Zobel M (1999) Small-scale plant species richness in calcareous grasslands determined by the species  
549 pool, community age and shoot density. *Ecography* 22:153-159

550 Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18

551 Prach K, Walker LR (2011) Four opportunities for studies of ecological succession. *Trends Ecol Evol* 26:119-123

552 R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for  
553 Statistical Computing, Vienna

554 Richter BS, Tiller RL, Stutz JC (2002) Assessment of arbuscular mycorrhizal fungal propagules and colonization  
555 from abandoned agricultural fields and semi-arid grasslands in riparian floodplains. *App. Soil Ecol.* 20:227-  
556 238.

557 Römermann C, Dutoit T, Poschlo P, Buisson E (2005) Influence of former cultivation on the unique  
558 Mediterranean steppe of France and consequences for conservation management. *Biol Conserv* 121:21-33

559 Schnoor T, Lekberg Y, Rosendahl S, Olsson P (2011) Mechanical soil disturbance as a determinant of arbuscular  
560 mycorrhizal fungal communities in semi-natural grassland. *Mycorrhiza* 21:211-220

561 Semelová V, Hejčman M, Pavlů V, Vacek S, Podrázský V (2008) The Grass Garden in the Giant Mts. (Czech  
562 Republic): Residual effect of long-term fertilization after 62 years. *Agric Ecosyst Environ* 123:337-342

563 Smith MD, Hartnett DC, Wilson GWT (1999) Interacting influence of mycorrhizal symbiosis and competition on  
564 plant diversity in tallgrass prairie. *Oecologia* 121:121:574-582

565 Smits NA, Willems JH, Bobbink R (2008) Longterm aftereffects of fertilisation on the restoration of calcareous  
566 grasslands. *Appl Veg Sci* 11:279-286

567 Sousa WP (1984) The Role of Disturbance in Natural Communities. *Annu. Rev. Ecol. Syst.* 15:353-391

568 Spiegelberger T, Deléglise C, DeDanieli S, Bernard-Brunet C (2010) Resilience of acid subalpine grassland to  
569 short-term liming and fertilisation. *Agric Ecosyst Environ* 137:158-162

570 Spiegelberger T, Hegg O, Matthies D, Hedlund K, Schaffner U (2006) Long-term effects of short-term perturbation  
571 in a subalpine grassland. *Ecology* 87:1939-1944

572 The Angiosperm Phylogeny Group (2009) An update of the Angiosperm Phylogeny Group classification for the  
573 orders and families of flowering plants: APG III. *Bot J Linn Soc* 161:105-121

574 Tomanek GW, Albertson FW, Riegel A (1955) Natural Revegetation on a Field Abandoned for Thirty-Three Years  
575 in Central Kansas. *Ecology* 36:407-412

576 Tscherko D, Hammesfahr U, Zeltner G, Kandeler E, Böcker R (2005) Plant succession and rhizosphere microbial  
577 communities in a recently deglaciated alpine terrain. *Basic Appl Ecol* 6:367-383

578 Van de Voorde TFJ, van der Putten WH, Gamper HA, Gera Hol WH, Martijn Bezemer T (2010) Comparing  
579 arbuscular mycorrhizal communities of individual plants in a grassland biodiversity experiment. *New*  
580 *Phytol* 186:746-754

581 Van der Heijden MGA, Horton TR (2009) Socialism in soil? The importance of mycorrhizal fungal networks for  
582 facilitation in natural ecosystems. *J Ecol* 97:1139-1150

583 Van Der Heijden MGA, Wiemken A, Sanders IR (2003) Different arbuscular mycorrhizal fungi alter coexistence  
584 and resource distribution between co-occurring plant. *New Phytol* 157:569-578

585 Van der Heijden MGA, Sanders IR (2002) Mycorrhizal Ecology, Springer-Verlag Berlin and Heidelberg GmbH  
586 & Co. K

- Veldman JW, Buisson E, Durigan G, Fernandes GW, Le Stradic S, Mahy G, Negreiros D, Overbeck GE, Veldman RG, Zaloumis NP, Putz FE, Bond WJ (2015) Toward and old-growth concept for grasslands, savannas, and woodlands. *Front Ecol Environ* 13: 154–162
- Vierheilig H, Coughlan AP, Wyss U, Piché Y (1998) Ink and Vinegar, a Simple Staining Technique for Arbuscular-Mycorrhizal Fungi. *Appl Environ Microbiol* 64:5004-5007
- Wang B, Qiu YL (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16:299-363
- Wardle DA (2006) The influence of biotic interactions on soil biodiversity. *Ecol Lett* 9:870-886.
- Wardle DA, Jonsson M (2014) Long term resilience of above- and below-ground ecosystem components among contrasting ecosystems. *Ecology* 95:1836-1849
- Warner NJ, Allen MF, MacMahon JA (1987) Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia* 79:721-730
- Wilson G, Hartnett D (1997) Effects of mycorrhizae on plant growth and dynamics in experimental tall grass prairie microcosms. *Am J Bot* 84:478-478
- Wong NK, Morgan JW, Dorrough J (2010) A conceptual model of plant community changes following cessation of cultivation in semi-arid grassland. *Appl Veg Sci* 13:389-402
- Zobel M, Moora M (1995) Interspecific competition and arbuscular mycorrhiza: importance for the coexistence of two calcareous grassland species. *Folia Geobot* 30:223-230

## Tables

Table 1: Aikake Information Criterion of Generalized Linear Mixed Models, one including Age as a fixed effect and Block as a random effect, the other including only Block as a random effect. Stars preceding variable names indicate that the model including age is better (i.e.  $\Delta AIC > 2$  ; Burnham and Anderson, 2004) and age can therefore be considered as affecting the variable.

	Variable	AIC <i>Age+Block</i>	AIC <i>Block</i>
Mycorrhizal root colonization	* <i>Brachypodium distachyon</i>	276.1	289.8
	* <i>Bromus madritensis</i>	344.2	368.5
	* <i>Carthamus lanatus</i>	274.7	286.0
	* <i>Carduus pycnocephalus</i>	187.0	198.1
Vegetation	*Species-richness	364.7	472.6
	*CSII	-50.5	40.8
	*HAI	-110.5	-14.9
	*Average height	351.5	410.0
	*Vegetation cover	430.7	474.5
Soil	*Carbon	69.2	76.8
	*pH	9.5	19.5
	C:N	23.2	25.0
	Nitrogen	3.1	-6.9
	Phosphorus	-54.8	-69.8
	Potassium	-30.8	-40.3

## Figure Captions

**Fig. 1** Study site and sampling design. a: location of La Crau area in France. b: location of study area in La Crau area. c: location of sites: the two steppe sites (ST-6000) and the field sites abandoned for 150 (AF-150), 35 (AF-35) and 2 (AF-2) years. Dark grey areas represent sampled abandoned fields. d: detailed scheme of design per sampling area, large circle represents the area prospected for individuals of the four species for mycorrhizal root colonization assessment, grey squares represent the three 2x2m quadrats where plant species abundances were recorded and black dots represent the three soil samples before pooling for soil physical and chemical analyses

**Fig. 2** Mean mycorrhizal root colonization for the four species in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Error bars represent standard error; bars having a common letter are not significantly different (Tukey;  $p > 0.05$ ). Numbers inside plots indicate the number of individual plants on which mycorrhizal root colonization was counted. Missing bars indicate that the species was not found in any plot of the abandoned field

**Fig. 3** Ordination plot of the Principal Component Analysis based on soil granulometry and nutrient content in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Arrows represent soil variables (coarse sand, fine sand, coarse silt, fine silt, clay, organic matter, C:N: Carbon/Nitrogen ratio; C: total carbon; N: total nitrogen; K<sub>2</sub>O: potassium, P<sub>2</sub>O<sub>5</sub>: Olsen phosphorus; CaO: Calcium oxide and pH). Polygons surround the points corresponding to one age class

**Fig. 4** Soil nutrient content in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Mean values  $\pm$  standard error of carbon (C), nitrogen (N), C/N ratio (C/N), phosphorus (P<sub>2</sub>O<sub>5</sub>), and potassium (K<sub>2</sub>O) in steppe (ST-6000) and abandoned fields (AF-2/35/150). Bars having a common letter are not significantly different (Tukey;  $p > 0.05$ )

**Fig. 5** Mean species richness per 4 m<sup>2</sup> (a), normalized Community Structure Integrity (b), Index Higher Abundance Index (c), average height (d) and percentage of vegetation cover (e) in steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Error bars represent standard error; bars having a common letter are not significantly different (Tukey;  $p > 0.05$ )

**Fig. 6** Ordination plot of the Correspondence Analysis based on vegetation abundances on steppe (white, ST-6000) and abandoned fields (grey, AF-2/35/150). Based on 54 relevés and 110 species, showing the 35 most correlated with the axes. Polygons surround the points corresponding to one age class